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Variations in germination and grain quality within a rust resistant common wheat germplasm as affected by parental CO₂ conditions

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Abstract

Parental conditions, such as temperature, soil moisture, nutrient availability, light and competition during plant growth and seed maturation, influence seed quality and germinability. Elevated CO₂ concentration can be also treated as a parental condition and should be considered when evaluating crop productivity under future climate conditions. Available information on the effect of parental CO₂ conditions on seed quality and germinability is limited, particularly for intra-population variations. Therefore, seeds of several entries of a rust resistant common wheat germplasm (*Triticum aestivum* L., AZ-MSFERS-82RR PI# 552988) grown under three CO₂ concentrations (350, 700 and 1000 ppm) were studied to determine the intra-population variation in seed germinability and grain quality, and the relationship between grain quality and germinability. Germination percentage was near 100% for all treatments, but different patterns in germination rate were found among entries: (1) both 700 and 1000 ppm CO₂ increased germination rate comparing with 350 ppm CO₂, (2) both 700 and 1000 ppm CO₂ reduced seed germination rate, and (3) 700 but not 1000 ppm CO₂ reduced germination rate. These variations were apparently entry-related, indicating the existence of intra-population variation in the response of germination rate to parental CO₂ conditions. Chemical constituents responded to increasing CO₂ concentration differently among entries, but the C/N ratio was similar among CO₂ treatments. A negative correlation between C content and germination rate was found. The importance of this correlation in seeds of other species should be evaluated because it may serve as an indicator for the effect of CO₂ enrichment on seed germinability. Because elevated CO₂ parental conditions may affect both seedling establishment and grain quality of crops, intra-population variations in the response of seed germinability and grain quality to CO₂ conditions should be considered in future breeding efforts.

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Keywords: Common wheat; Elevated CO₂; Germination; Grain quality; Parental condition

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1. Introduction

Carbon dioxide enrichment is an important component of potential global climate change. While the effect of CO₂ enrichment on plant growth and crop yield have been extensively studied (Bazzaz, 1990; Poorter et al., 1996), data regarding its impact on seed germination and plant regeneration are few (Andalo et al., 1996; Sanhew et al., 1996).

It has been well documented that parental conditions, particularly temperature and soil moisture during plant growth and seed maturation, influence seed quality and germinability (Guterman, 1980/1981; Peters, 1982; Plett and Larter, 1986; Drew and Brocklehurst, 1990; Hume, 1994; Lacey, 1996). Other factors, such as nutrient availability, light and competition, also affect seed germination (Aarssen and Burton, 1990; Wulff, 1993). Crop and horticultural species may be more sensitive to parental conditions than those in natural ecosystems (Beckstead et al., 1996). Germination of seeds produced under different parental CO₂ conditions should also be considered when evaluating crop productivity under future climate conditions.

The effect of CO₂ enrichment during plant growth and seed production and its influence on seed germination can be species- or population-specific (Kimball, 1983; Cure and Acock, 1986; Curtis et al., 1994; Navas et al., 1995), however, no report regarding intra-population variation is available. The relationship between grain quality of seeds produced under elevated CO₂ and their germinability is also unknown. A common wheat (*Triticum aestivum* L. cv. AZ-MSFERS-82RR) germplasm grown under three CO₂ concentrations were studied to determine the intra-population variation in seed germinability and grain quality. We hypothesized that intra-population variations exist in this germplasm in terms of seed germinability and grain quality in response to CO₂ enrichment. These variations can be used in future breeding for the selection of wheat suitable under elevated CO₂ conditions.

2. Materials and methods

2.1. Seed sources

Seeds of a rust resistant common wheat germplasm, AZ-MSFERS-82RR PI# 551988, were obtained from the USDA-ARS germplasm collection at Aberdeen, Idaho. This germplasm was the result of hand crossing of numerous lines of common wheat with known resistance to rust and was expected to be used as a source of nonspecific (horizontal) resistance in epidemic areas (Thompson, 1983). This germplasm exhibits high diversity in maturity, plant type, seed class, and agronomic behavior. Seeds were planted in a glasshouse in 1994 for seed production and individual plants were labeled and given an entry number. Seeds were harvested from entries with normal plants only and planted again in three replications in the fall of 1994. Entries with plants that failed to flower or had malformed seed heads were discarded. During plant growth, entries that exhibited visual differences among replications were discarded and seeds from those without visual variations were harvested. The above procedures resulted in six entries, 1, 6, 13, 17, 19, and 21, which were used in the experiment. Differences in plant height, seed maturity, and grain yield among entries were observed, which indicated that those entries were likely genetically diverse and prompted this study. Given the fact that each entry arose from a single-seed descent, each individual entry should be genetically pure even though variations among seeds with different maturity and/or positions in the seed heads are unavoidable.

2.2. Growth conditions and CO₂ treatments

Experiments were initiated in the spring of 1995. Five seeds from the same plant of each entry were randomly selected. These seeds were surface sterilized for 5 s in 10% ethanol followed by 30 s in a 1:10 dilution of chlorox. They were then rinsed with distilled water and allowed to dry. On the same day, each seed was planted in a 10 in. pot filled with Redi-earth (W.R. Grace, Inc., Tifton, USA), a peat-vermiculite type media containing

starter fertilizer. Pots were placed in glasshouse bays as described below. Seedlings emerged approximately 8–9 days after planting. Plants were watered with tap water as needed and fertilized weekly with 250 ml, full strength ‘Hoagland’ solution per pot 3 weeks after planting. Seeds were harvested when all plants had seeded and seeds were dry, about 3.5 months after planting. They were then hand cleaned, put in paper bags, and stored in seed storage vault until used in the germination test.

Three adjacent glasshouse bays were used with temperatures maintained at approximately 25 °C during the day and 18 °C during the night. The atmospheric CO₂ concentrations were maintained at ambient (365), 700 or 1000 ppm, respectively. Tischler et al. (1998) provided detailed descriptions of conditions in the glasshouse bays and a brief summary is provided here. The CO₂ concentrations were maintained by constant, automatic injection and the actual values during the experiment averaged 391.3, 683.5 and 1009.1 ppm, respectively. The average daily temperatures were 21.3, 21.6 and 21.4 °C, respectively, for the three glasshouse bays, and the within-glasshouse variation was minimal. Daily mean integrals of light intensity intercepted were 17.4, 16.9, and 16.3 mol m⁻² per day in the three bays, respectively. Continuous measurements at 20 min intervals showed that temperature, light intensity, and vapor pressure deficit were very similar among glasshouses (Tischler et al., 1998). There were five replicates (pots) for each entry and CO₂ concentration. The within-glasshouse variations were also reduced by frequent re-arrangement of pots. Seedlings were watered as needed to avoid water stress.

Total seed number and total seed production per plant were determined after harvest. Seeds were stored in a seed storage vault until use. Seed mass (weight per seed) was then calculated based on fresh weight due to the limited amount of seeds. This was done 1 year after seed harvest with the assumption that seeds had reached an equilibrium with the atmosphere thus minimizing variations in water content among seeds.

2.3. Germination test

A germination test was conducted 14 months after seed harvest using seeds from each of the five plants as a replicate. The experiment was a complete randomized design. Fifty seeds were placed on 1 mm thick germination paper on slant boards (Booth and Griffith, 1994). Seeds were incubated under 12:00 h light:12:00 h darkness for 28 and 7 days in growth chambers at 5 and 20 °C, respectively. Seed germination was checked daily and seeds were considered germinated when the radicle was 5 mm long.

2.4. Grain quality analysis

Fifty seeds from each replicate were used for grain quality analysis and the same five replicates in the above experiment were used. Seeds were oven dried at 60 °C for 48 h and ground. Three sub-samples were weighed into crucibles (0.500 ± 0.002 g) and dry-ashed at 550 °C for 4 h. They were then digested in 6 M HCl, filtered through one layer of Whatman No. 40 filter paper, and diluted to 100 ml using deionized water. The P content was determined on an aliquot of this solution using the vanadomolybdophosphoric yellow method (Jackson, 1958). Ca, Mg and K contents were determined on a separate aliquot using a Perkin-Elmer model 2100 atomic absorption spectrophotometer.

Seeds used for C and N analysis were oven dried at 60 °C for 48 h both before and after grinding. Two sub-samples were analyzed using a Carlo-Erba model NA2100 combustion furnace.

2.5. Data analysis

Several germination-related indices were used to measure the speed of germination because of the high germination percentage among entries and treatments. Germination rate index (GRI) was calculated as the sum of germinated seeds for each day divided by days (Maguire, 1962) and then adjusted by dividing by G. Days to 50% germination (D50) was transformed by $(1 - (1/(x+1)))$ (Edwards and El-Kassaby, 1995). Peak value (PV) was defined as the maximum of cumulative

germination percentage divided by days and transformed by $\sqrt{0.5 \times}$ (Czabator, 1962; Thompson and El-Kassaby 1993). Data for seed germination and grain quality were analyzed with ANOVA in a complete randomized design with five replicates and means were separated with LSD (Snedecor and Cochran, 1980). Differences between means were considered significant when $P = 0.05$. Regression analysis between GRI and grain chemical contents were conducted and the best-fit equations were selected.

3. Results

3.1. Seed production

The effect of CO₂ concentration on seed production varied among entries. Total seed production per plant (both number and yield) was dramatically enhanced by both 700 and 1000 ppm CO₂ concentrations for Entry 17 (Table 1). Seed production was reduced by 1000 ppm CO₂ for Entries 1 and 21; Entries 6, 13 and 19 were not affected by CO₂ concentration. Seed mass was generally not affected by CO₂ concentration except in Entry 6, where 700 ppm, but not 1000 ppm CO₂ concentration, slightly enhanced seed mass (<5%, data not shown).

3.2. Seed germination

Final germination percentage at both incubation temperatures was near 100% and similar among CO₂ treatments for all entries. Most seeds germinated between thermal time (with a base temperature of 0 °C) 40 and 60 °C day. The effect of CO₂ on seed germination was reflected in germination rate. The thermal time required for germination was similar at 5 and 20 °C incubation temperatures. Therefore, only the germination rate of seeds incubated at 5 °C was reported here (Fig. 1, Table 2). Among the three parameters used for germination rate measurement, GRI was a more sensitive measure on the speed of germination than D50 or PV. An enhanced germination rate by CO₂ enrichment was observed in Entries 1 and 6. A reversed effect was shown in Entries 17 and 19.

Table 1

Total seed number and seed yield per plant of six entries of a common wheat germplasm produced under three levels of CO₂

Entry	CO ₂ concentration	Seed number	Seed yield (f.w.g)
Entry 1	350 ppm	361 a	16.6 a
	700 ppm	366 a	18.1 a
	1000 ppm	222 b	10.2 b
<i>P</i> -value		< 0.001	< 0.001
Entry 6	350 ppm	326 a	15.6 ab
	700 ppm	343 a	17.1 a
	1000 ppm	271 a	12.4 b
<i>P</i> -value		0.100 (NS)	0.035
Entry 13	350 ppm	156 a	7.3 a
	700 ppm	239 a	11.0 a
	1000 ppm	216 a	9.7 a
<i>P</i> -value		0.186 (NS)	0.221 (NS)
Entry 17	350 ppm	108 b	3.9 b
	700 ppm	347 a	13.7 a
	1000 ppm	305 a	12.1 a
<i>P</i> -value		< 0.001	< 0.001
Entry 19	350 ppm	283 a	15.5 a
	700 ppm	185 a	10.0 a
	1000 ppm	195 a	10.4 a
<i>P</i> -value		0.331 (NS)	0.310 (NS)
Entry 21	350 ppm	303 a	15.5 a
	700 ppm	252 ab	10.0 a
	1000 ppm	233 b	10.4 a
<i>P</i> -value		0.041	0.065 (NS)

Means with the same letter within a parameter and entry are not significantly different at $P = 0.05$.

For Entries 13 and 21, germination was delayed by 700 ppm CO₂, but germination rate increased as CO₂ concentration reached the level of 1000 ppm. The regression between GRI and P, Ca, Mg, N and weight per seed was not significant. However, GRI decreased with increasing C content ($P = 0.051$, $R^2 = 0.17$, Fig. 2).

3.3. Grain quality

Each of the chemical constituents responded differently to increasing CO₂ concentration among the six entries (Table 3). CO₂ concentration did not affect P content in seeds of three entries (Entries 6, 13 and 21). Increasing CO₂ reduced the P content in Entry 19, but P content for Entries 1 and 17 was higher under 350 and 1000 ppm CO₂ than 700 ppm. Increasing CO₂ concentration generally reduced Ca content of seeds. For Entry

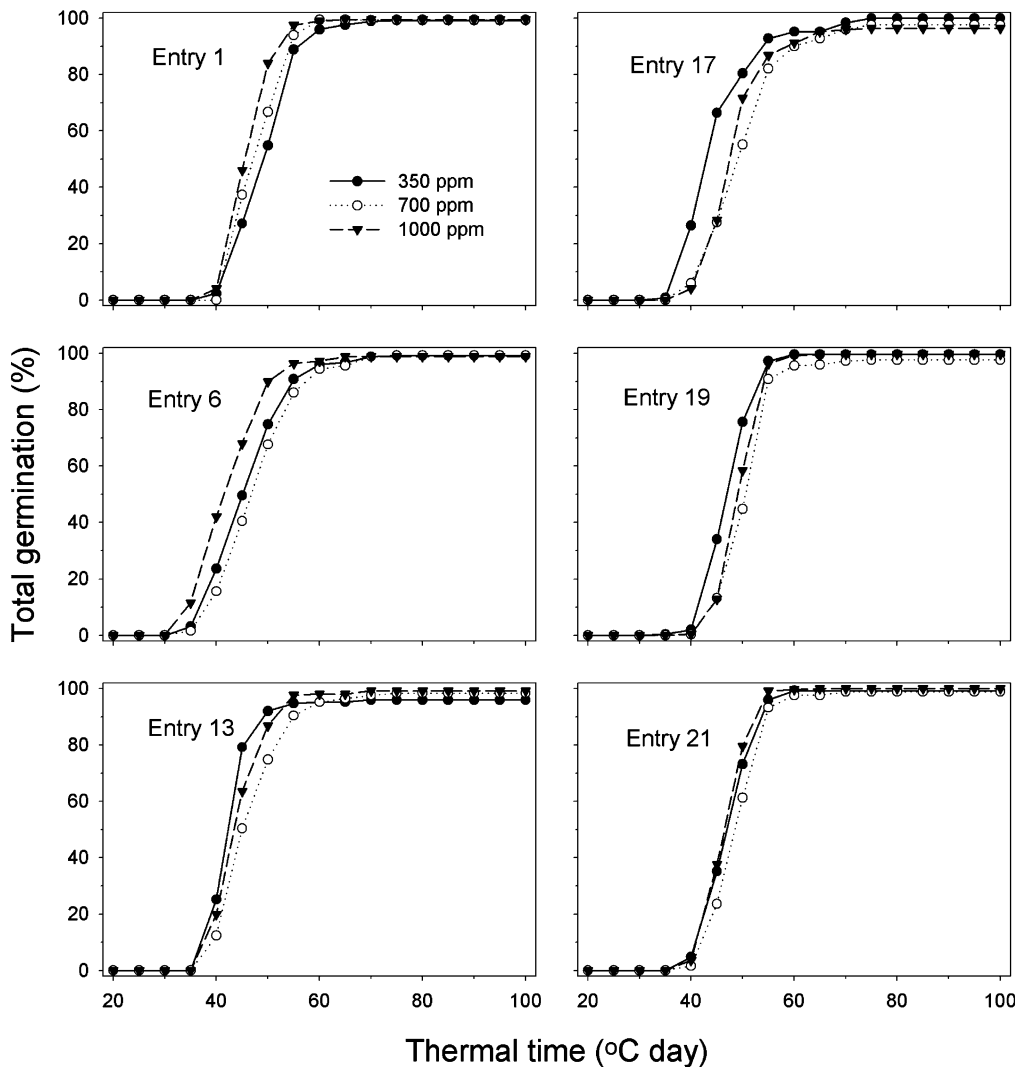


Fig. 1. Germination profiles of six entries of a common wheat germplasm produced under three levels of CO_2 and incubated at 5°C between thermal time of 20 and 100°C day .

17, Ca content was higher for seeds grown under 350 than 700 and 1000 ppm. The influence of CO_2 concentration on Mg content was similar to that on P, except for Entry 1, in which the treatment effect was not significant due apparently to variations among replicates, and for Entry 6, in which Mg content was reduced by increasing CO_2 concentration. Increasing CO_2 reduced K content in three entries (Entries 1, 13 and 17). Increasing CO_2 concentration did not affect seed C or N for most entries. Even when this effect was significant, (e.g.

C content for Entry 6), the reduction in C or N content by enhanced CO_2 concentration was less than 1%. The ratio of C/N was not affected by increasing CO_2 in all entries.

4. Discussion

Species- or genotype-specific response in germination to elevated CO_2 concentration has been reported in several species among the limited

Table 2

GRI days to 50% germination (D50), and PV of six entries of a common wheat germplasm produced under three levels of CO₂ and incubated at 5 °C

Entry	CO ₂ concentration	GRI (% per day)	D50 (day)	PV
Entry 1	350 ppm	9.8 b	10.2 a	8.1 b
	700 ppm	10.1 ab	10.0 a	8.5 ab
	1000 ppm	10.4 a	9.5 a	9.0 a
<i>P</i> -value		0.038	0.102 (NS)	0.005
Entry 6	350 ppm	10.6 b	9.4 ab	8.6 a
	700 ppm	10.2 b	9.8 a	8.0 a
	1000 ppm	11.4 a	8.6 b	9.0 a
<i>P</i> -value		0.017	0.047	0.085 (NS)
Entry 13	350 ppm	11.2 a	9.0 a	9.6 a
	700 ppm	10.4 b	9.4 a	8.3 a
	1000 ppm	10.8 ab	9.4 a	9.2 a
<i>P</i> -value		0.023	0.300 (NS)	0.052 (NS)
Entry 17	350 ppm	10.8 a	9.4 b	8.6 a
	700 ppm	9.7 b	10.4 a	7.6 a
	1000 ppm	9.9 b	10.0 a	7.9 a
<i>P</i> -value		0.011	0.012	0.187 (NS)
Entry 19	350 ppm	10.2 a	9.8 b	8.8 a
	700 ppm	9.5 b	10.8 a	8.4 a
	1000 ppm	9.7 b	10.2 ab	8.8 a
<i>P</i> -value		< 0.001	0.016	0.133 (NS)
Entry 21	350 ppm	10.2 a	10.0 a	8.7 b
	700 ppm	9.8 b	10.2 a	8.5 b
	1000 ppm	10.3 a	10.0 a	9.0 a
<i>P</i> -value		0.019	0.397 (NS)	0.010

Means with the same letter within a parameter and entry are not significantly different at $P = 0.05$.

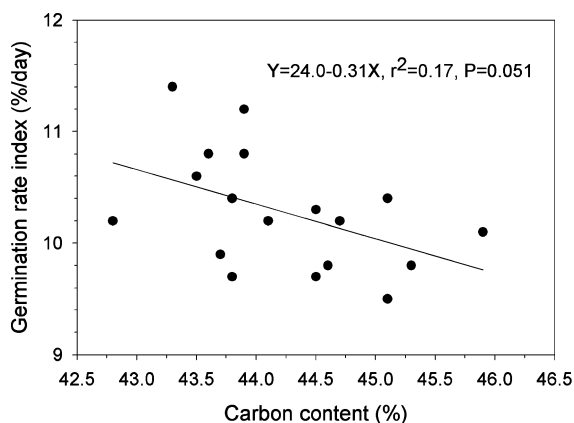


Fig. 2. The relationship between GRI and seed carbon content of a common wheat germplasm produced under three levels of CO₂ enrichment and incubated at 5 °C. Data of the six entries and three CO₂ treatments were pooled.

studies (Wulff and Alexander, 1985; Garbutt et al., 1990; Andalo et al., 1996). Similar germination

percentage between normal and elevated CO₂ parental conditions were found in winter wheat (cv. Hereward) (Sanhewu et al., 1996) and red brome (*Bromus rubens* L.) (Huxman et al., 1998), which agrees with results from the current study. On the other hand, reduced seed viability under elevated CO₂ was found in mouseear cress (*Arabidopsis thaliana* L.) (Andalo et al., 1996).

The six entries of common wheat in our study responded differently to CO₂ enrichment in their germination rate. Three patterns were found: (1) both 700 and 1000 ppm CO₂ increased germination rate comparing to 350 ppm, (2) both 700 and 1000 ppm CO₂ reduced seed germination rate, and (3) germination rate was reduced by 700 but not 1000 ppm CO₂. These variations were apparently entry-related, indicating the existence of intra-population variation in the response of germination rate to parental CO₂ conditions.

Table 3

Grain quality of six entries of a common wheat germplasm produced under three levels of CO₂

Entry	CO ₂ concentration	P (ppm)	Ca (ppm)	Mg (ppm)	K (ppm)	C (%)	N (%)	C/N
Entry 1	350 ppm	5056 a	292 a	1456 a	5305 a	45.3 a	2.7 a	17 a
	700 ppm	4582 b	227 b	1268 a	4840 b	45.9 a	2.5 a	19 a
	1000 ppm	5127 a	209 b	1390 a	5068 ab	45.1 a	2.4 a	19 a
P-value		0.039	< 0.001	0.101 (NS)	0.008	0.385 (NS)	0.284 (NS)	0.302 (NS)
Entry 6	350 ppm	4589 a	239 a	1448 a	4425 a	43.5 a	2.8 a	16 a
	700 ppm	4581 a	189 b	1279 b	4457 a	42.8 b	2.4 a	18 a
	1000 ppm	4748 a	176 b	1290 b	4464 a	43.3 a	2.4 a	18 a
P-value		0.339 (NS)	< 0.001	0.014	0.961 (NS)	0.011	0.961 (NS)	0.140 (NS)
Entry 13	350 ppm	5545 a	211 a	1517 a	5276 a	43.9 a	2.6 a	17 a
	700 ppm	5550 a	189 a	1510 a	5007 a	43.8 a	2.8 a	16 a
	1000 ppm	5693 a	150 b	1505 a	4565 b	43.6 a	3.2 a	14 a
P-value		0.721 (NS)	0.001	0.984 (NS)	0.001	0.268 (NS)	0.187 (NS)	0.492 (NS)
Entry 17	350 ppm	5446 a	298 a	1671 a	6075 a	43.9 a	2.2 a	20 a
	700 ppm	4760 b	147 b	1260 c	5205 b	43.8 a	2.2 a	21 a
	1000 ppm	5357 a	160 b	1415 b	5446 b	43.7 a	2.3 a	19 a
P-value		0.021	0.003	0.002	0.006	0.632 (NS)	0.693 (NS)	0.573 (NS)
Entry 19	350 ppm	4775 a	207 a	1456 a	4802 a	44.1 a	2.5 a	18 a
	700 ppm	4346 b	250 a	1331 ab	4293 a	45.1 a	2.5 a	18 a
	1000 ppm	4508 b	199 a	1221 b	4472 a	44.5 a	2.4 a	19 a
P-value		0.008	0.677 (NS)	0.012	0.054 (NS)	0.262 (NS)	0.819 (NS)	0.776 (NS)
Entry 21	350 ppm	4398 a	239 a	1241 a	4256 a	44.7 a	2.4 a	19 a
	700 ppm	4539 a	204 b	1297 a	4234 a	44.6 a	2.6 a	18 a
	1000 ppm	4613 a	182 c	1227 a	4262 a	44.5 a	2.3 a	20 a
P-value		0.251 (NS)	< 0.001	0.279 (NS)	0.917 (NS)	0.054 (NS)	0.500 (NS)	0.563 (NS)

Means with the same letter within a parameter and entry are not significantly different at $P = 0.05$.

The protein content or N was reduced in barley (*Hordeum vulgare* L.) and wheat grains (Conroy et al., 1994; Thompson and Woodward, 1994; Blumenthal et al., 1996; Sæbø and Mortensen, 1996), and fruits of strawberry (*Fragaria x ananassa* Duch. cv. 'Elsanta') (Chen et al., 1997) produced under elevated CO₂, but not in spring wheat (cv. 'Sport'), oat (cv. 'Kapp') (Sæbø and Mortensen, 1996), or rice (*Oryza sativa* cv. Jarrah) (Seneweera et al., 1996). Starch content was not affected by elevated CO₂ in wheat (Tester et al., 1995; Blumenthal et al., 1996), but was enhanced in rice (Seneweera et al., 1996). The N or C content in the six entries of common wheat in our study was not affected by CO₂ parental conditions, which agrees with previous studies.

The C/N ratio is an important parameter in grain quality analysis. The six entries of common wheat in our study did not exhibit differences in C/N ratio among CO₂ treatments. However, a negative correlation between C content and ger-

mination rate was found. The importance of this correlation in grains or seeds of other species needs to be evaluated because it may serve as an indicator for the effect of CO₂ enrichment on seed germinability because the C/N ratio could be reduced (e.g. in spring wheat and barley, Thompson and Woodward, 1994), or enhanced (e.g. in red brome, Huxman et al., 1998) by elevated CO₂. It is expected that crops and native plants responding differently to changing environmental conditions as the evolution of native plants are directed by natural selection while agronomic species are selected for high harvest index and grain quality characteristics.

Intra-population variations for several mineral contents were observed in our study. In rice, elevated CO₂ increased Ca concentrations, but reduced that of P and Mg; a close correlation between P and Mg was also found (Batten, 1994; Seneweera et al., 1996). The content of K was slightly reduced in strawberry possibly due to a

dilution effect of increased dry matter content (Chen et al., 1997).

A survey of 430 observations on the yield of 37 species indicates that on average, crop yield will probably increase by 33% when grown under elevated CO₂ (Kimball, 1983). Even though the effect of CO₂ on grain yield is species or population specific (Kimball, 1983; Cure and Acock, 1986; Curtis et al., 1994; Navas et al., 1995), no decreased effect has been reported. Among the six entries of common wheat tested in our study, several patterns of yield response to elevated CO₂ were observed, including a reduction by 1000 ppm CO₂ in grain yield for one entry, indicating an intra-population variation. It should be noted that the cloudy weather condition during plant growth in February might have reduced the variation in grain yield among CO₂ treatments, as shading reduced wheat (cv. Mercia) grain yield (Mitchell et al., 1996). This may also be true for seed mass since in only one of the six entries in our study was seed mass slightly enhanced by elevated CO₂. However, observed differences in plant height, biomass and seed maturity among CO₂ treatments (data not shown) indicate that the cloudy condition did not eliminate CO₂ effects. In other species, such as rice (cv. Jarrah) (Seneweera et al., 1996), wheat (cv. Hereward) (Wheeler et al., 1996a,b), and several native species (Garbutt and Bazzaz, 1984; Farnsworth and Bazzaz, 1995), seed mass was enhanced by elevated CO₂. A reversed case was with red brome, which had less total mass under elevated parental CO₂ concentration than those under ambient conditions (Huxman et al., 1998). Even when the yield and mass of rice (*O. sativa* L. cv. Nipponbare) were similar among CO₂ treatments, the percentage of ripened grain was reduced dramatically by 1200 ppm of CO₂ (Morokuma et al., 1996).

The hypothesis that intra-population variations exist in this germplasm in terms of seed germinability and grain quality in response to CO₂ enrichment has been accepted. In natural ecosystems, plant regeneration and seedling emergence from seeds produced under elevated CO₂ conditions may have major impacts on community composition and ecosystem processes (Bazzaz et al., 1992; Jackson et al., 1994). For crops, elevated

CO₂ parental conditions may affect both seedling establishment and grain quality. Therefore, intra-population variations in the response of seed germinability and grain quality to CO₂ conditions should be considered in breeding efforts.

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